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NEW FORMS OF VOLVOX

BY J. H. POWERS

WITH FOUR PLATES

(Studies from the Zoological Laboratory, the University of Nebraska, under the direction of Henry B. Ward, No. 75.)

The typical genera of the Volvocineae, *Pandorina*, *Eudorina*, and *Volvox*, are cosmopolitan and well known types. It has even been suggested that *Volvox* at least is so cosmopolitan that new species are not likely to be met with. Yet within a few years the writer has found, in one vicinity and without especial search, new forms, or at least decidedly new phenomena, in connection with each one of the above genera. *Pandorina* has shown a wholly unwarranted method of asexual reproduction, a method in which single cells, instead of all of the cells, gave rise to new colonies, suggesting, at least, the parthenogenesis of *Volvox*. *Eudorina* has shown all possible transition gradations between its proper self and the newly discovered form—supposed to be a separate genus—of *Pleodorina*, the four “somatic cells” of the latter proving somatic or not somatic according to the degree of their differentiation in size.¹

Lastly, *Volvox*, upon the two occasions of its occurrence within the writer's observation, has differed so fundamentally from hitherto described forms as to suggest the necessity of specific separation. Even in the two instances in which it has occurred, in ponds but a few miles from each other, the forms were not only new, but they differed from each other in certain important respects as much as all previously described forms have differed in regard to the same characters. Unfortunately, in the case of both of these finds, it was impossible to follow the species for any length of time to note constancy or inconstancy throughout changing seasonal conditions. One pond was dry within a week after the *Volvox* was noted. The other was inconvenient of access, and the organism was not

¹I owe the first demonstration of this fact to my former pupil and assistant, Mr. George R. LaRue of Crete, Nebraska.

found until late in the season. For these reasons I have delayed describing the forms, hoping to hit upon more material and work out more fully the relation of the types to the known forms of the genus. But our seasons are irregular and *Volvox*, everywhere precarious, seems but an occasional visitor with us. A description of the forms as found may draw attention to the possibilities that await a fuller search elsewhere. Moreover, the forms are not uninteresting taken by themselves. I will describe the two forms separately, comparing each with the forms of the genus hitherto recorded, *viz.*, *Volvox globator*; *V. aureus* (= *V. minor*), with its important variety described by Klein;¹ *V. carteri*, the doubtful species described from India; and lastly *V. tertius*, discovered and described by Arthur Meyer² in Germany in 1896.

The material upon which the description of the first form is based consists at present of thirty mounted slides, containing several thousand colonies and displaying in abundance all phases of sexual and asexual reproduction. The collection was made several years ago, at about midsummer, in the shallow remnant of a prairie pond. It was without drainage and contained considerable alkali. The pond was exceedingly variable, covering several acres during a good part of some seasons, while remaining nearly or quite dry throughout others. It is a favorite resort of water birds during their migrations, and the *Volvox* may thus easily have been introduced from a distance. The material, after considerable examination in the fresh state, was fixed successfully in a number of reagents, the most perfect results being obtained with Flemming's strong formula diluted with several volumes of water. Stains worked easily and well, and mounts were made both in glycerine and balsam, chiefly in the former.

Of a number of features in which the *Volvox* in question differs from the members of the genus already described, the most interesting is the manner of formation of the sperm cells. These elements arise in all the above mentioned forms by the rapid division of enlarged cells of a parent coenobium. Sperm platelets are thus formed, containing variable numbers of sperms, and lying, until

¹Ludwig Klein: Neue Beiträge zur Kenntniss der Gattung *Volvox*, Berichte d. deutschen botanischen Gesellschaft, VII: 42.

²Arthur Meyer: Die Plasmaverbindungen und die Membranen von *Volvox globator*, *aureus*, und *tertius*, mit Rücksicht auf die thierische Zellen, Botanische Zeitung, XI and XII. 1896.

their final extrusion, within the common wall of the parent colony. The number of such sperm platelets may vary within wide limits. In *V. globator* and *V. carteri* it remains but few. In *V. aureus* and *V. tertius* it may become very great, until in rare cases of so-called "Sphaerosira colonies" of *V. aureus* two-thirds of the original number of the cells of the colony (1,000 to 1,100 in all, according to Klein) may be transformed into sperm mother cells and so ultimately into sperms. It should be noted, however, that even in such cases the typical character of the colony is preserved. It retains its free locomotion and especially its polarity. The sperm bundles are most numerous at the posterior pole, diminishing toward the anterior pole, which always remains free from them. The sperms, too, do not develop simultaneously; those at the posterior pole are developed and discharged first.

In the form which I am to describe, the phenomena are so different as, at first sight, to appear unrelated. Not a single instance could be found of a sperm platelet developing at the periphery of a free-swimming, mature colony. I examined many hundreds, if not thousands, of the living coenobia, and have also examined every coenobium of suitable development among my mounted preparations, probably not less than a thousand in all. The great majority are in sexual reproduction, yet not an instance of typical sperm production occurs. Instead I meet everywhere, within the older coenobia, with daughter colonies, or with what look like daughter colonies, every cell of which gives rise to a sperm platelet. (Pls. XII and XIII, figs. 7, 11, 12, 14, 15, 16, 17.) I am obliged to choose a new term to designate these premature, exclusively reproductive, and exclusively male colonies, if such they truly are. The name "sperm colony" would be most natural, had it not been applied by several writers to the single sperm platelet; while the term "male colony" has been applied to developed and usually independent coenobia whose reproductive cells become sperms only, instead of eggs or parthenogonidia. I choose for this purpose the designation "sperm spheres," or the phrase "pure male colony." As already suggested, I find this method of sperm production invariable. All in all I have certainly examined hundreds of sperm spheres in their mature condition,—*i. e.*, made up of platelets of ciliated sperms,—and of the more or less immature stages I have examined many hundreds more; yet among them all I have been unable to find a single "somatic

cell";¹ every cell, or every "individual" of the young colony, invariably becomes a sperm mother cell; none remain as ova; each becomes a platelet of sperms. The entire uniformity of this method is, if possible, even more significant than its novelty. And it is this fact which, under any interpretation which may be put upon it, separates this form of *Volvox* sharply from the others which most nearly approach it.

Two very different interpretations may, in fact, be placed upon this new instance of sperm development. We may, on the one hand, consider it an instance of acceleration and, in a sense, hypertrophy: acceleration, because the sperms are matured in very young colonies which pass all their life within the parent coenobium; hypertrophy, because, instead of a few or even the majority of the cells becoming sperm bundles, all of them become sperm bundles. On the other hand we may, in a measure, reverse our mode of interpretation and consider these sperm spheres, not as instances of acceleration, but of retardation in sperm production; they become, if thus viewed, not true colonies at all, but instances of the multiplication of primary reproductive cells—"spermogonia"—comparable to that which takes place in the metazoon testis. As we shall see later there are facts which point toward both of these interpretations, and perhaps the majority point toward the latter. Doubtless these two hypotheses are not, in truth, as different as they really seem—not, that is, for an organism on the developmental plane of *Volvox*. None the less, they are not one and the same, and from the standpoint of our definitions they make a great difference; the one throws this *Volvox* back closer to the Protozoa and relates it far more closely to *Eudorina*, the other makes it quite violently metazoon. For the present let us assume, as the least radical, the first of these hypotheses, *viz.*, that these sperm spheres are young colonies disintegrating wholly

¹I shall deliberately use, in this paper, such expressions as "somatic cells," "reproductive cells," etc., and I shall also use, with equal freedom, the terms "colony," "coenobium" and the like. Such expressions are flatly contradictory, in a sense; but so are the facts. They confuse no one familiar with the different points of view from which *Volvox* may be considered. The very beauty of *Volvox* and its group lies in the happy way in which they override "fundamental distinctions." Out of the seeming chaos, therefore, of terms—terms old and terms new, terms botanical and terms zoological, terms metazoon and terms protozoon,—I choose those most convenient and useful for the context in question.

into sperms, and make comparison with the known forms which most nearly approach it.

These forms are *Volvox tertius* as described by Meyer on the one hand, and, more particularly, the extreme form of *V. aureus* as described by Klein on the other. The facts presented by these types are very important for the understanding of the form I have discovered, for, if the hypothesis we are assuming be correct, they certainly constitute connecting links between it and the more typical forms of the genus. A brief résumé of the facts recorded by Klein will suffice equally well for both forms, the two being much alike in the matter of sperm production and Klein's description being much the more adequate. Probably, too, the variation which he found in *V. aureus* was more extreme, and resembled more the form found by the author than did *V. tertius* found by Meyer.

After spending much time in the study of the genus, and especially in investigating the variation of the species *V. aureus* in diverse localities and under diverse conditions, Klein published an extended monograph¹ upon the subject. In this he recorded a considerably wider range of variation for *V. aureus* than had hitherto been known. He showed conclusively, what had been already suspected, that the species was not necessarily, though it was typically, dioecious, and he increased considerably the number of sperm platelets which might be found in a single colony. The results of his extended research did not, however, go farther than this. After the close of his own investigations, however, he received a few prepared slides from a friend in Marburg, which showed a form of *V. aureus* far more suggestive of the Nebraska type. From his description and figures we gather that it was a small representative of the species (approximately 250 to 350 μ), this fact being due rather to a meagre development of the gelatinous matrix than to a reduction in the number of cells, or the size of the cells, in the colonies. The surprising fact, however, was the great precocity of the development of the daughter colonies while within the parent coenobia. They showed the ordinary cell-numbers of the species *V. aureus*, but they became of rather large size for young colonies, and showed a surprising acceleration in the development of reproductive cells.

¹Ludwig Klein: Morphologische und biologische Studien über die Gattung *Volvox*. Pringsheim's Jahrbücher für wissenschaftliche Botanik, XX: 133.

Ova reached a considerable size within the young coenobia, a size much beyond the ordinary, while the sperm platelets were frequently constituted of completely developed, ciliated sperms. These sperms and the platelets were a little smaller than is typical for the species *V. aureus*, but not smaller than is sometimes found. The only noticeable peculiarity was the invariable number of sperms in a platelet,—thirty-two,—instead of the usually variable assortment of large and small bundles.

The apparent resemblance of this interesting variation (which in these respects runs nearly parallel to the new species *V. tertius*) to the form found by the author is plain. In each we have an absence of sperm platelets in the original mother (grandmother?) coenobium. In each the sperm platelets, or at least a part of them, are formed and matured in daughter colonies, while within the original coenobium. In each we find, if we count the sperm bundle as the homologue of a colony, in the words of Klein, “*drei in einander eingeschachtelte Generationen; von denen jede vollkommen ausgebildet ist.*” In each we have the “*gräuelvolles Familienbild*” presented by the possibility that, within the body of the grandmother volvox, sperms should fertilize ova which stand to them in the relation of grand aunts. For ova are present in the older coenobia side by side with the precocious daughter colonies.

But a closer comparison shows at once that the points of difference are as many and even more significant than are the points of similarity.

In Klein's *V. aureus* colonies there was an irregular but general acceleration in the development of all reproductive cells, sperms, ova, and, presumably, parthenogonidia. In the form I am describing there is an actual and general retardation in the development of parthenogonidia greater than seems to take place in any other described *Volvox*, and there is at least no acceleration of the ova. I can never distinguish between ova and parthenogonidia in the undischarged daughter colonies. The development of sperms only is hastened, if such be the true interpretation, and, as we shall see, they are discharged from the “*individuals*” that produce them before these “*individuals*,”—the sperm spheres,—are born. Here lies a difference that separates the two cases widely. The daughter colonies described by Klein, although not observed by him in the living state, were, he assumed, still capable of an independent existence and were destined to escape from their parent coenobia and lead

such an existence, even though some of their mature sperm platelets should have become free and functional before their birth. I paid careful attention to this point when examining the living material. But an extended search did not discover a single sperm sphere in the free-swimming condition. On the other hand I did find sperm spheres which were breaking up into their component sperm bundles while still within the parent coenobium. The disruption begins by a more or less general loss of form and shifting of position of the individual bundles due to the action of their cilia, after which they escape, singly or a few at a time. My permanent preparations show an abundance of such stages. (Pl. XIII, fig. 17.) I regret that I did not make the experiment of freeing these sperm spheres artificially, to see whether or not they were capable of locomotion as a whole. In any case such motion is not natural to them, although the spheres, just before the final cell divisions, do show cilia, or at least rudiments of them. (Pl. XIII, fig. 14. The cilia could be made out with difficulty and do not show in the figure.) Correlated with the entire loss of somatic cells and of the power of independent existence goes the loss, or absence, of another otherwise universal character of *Volvox* colonies, viz., their polarity. Even Klein's prematurely developed daughter colonies, which, as he says, certainly passed an unwonted amount of their existence within the parent coenobium, yet showed distinctly the polar differentiation. Many of them are figured as ellipsoid, and they evidently all retain the characteristic area of exclusively somatic cells at one end. Whether or not the sperms ripened, as usual, in succession, from the more reproductive toward the somatic pole, his figures do not show, but had it been otherwise he probably would have mentioned the fact. As above suggested, no trace of this polarity seems to be retained by the sperm spheres which I am describing. The sister coenobia, which often develop side by side with them in the same parent, show such polarity strongly. (Pl. XI, figs. 1 and 3, and pl. XII, figs. 7, 8 and 9.) They are usually strongly ellipsoidal and their reproductive anlagen are always confined to one-half or two-thirds of the ellipsoidal area. The pure male colonies, on the contrary, are characteristically spherical in form even from the first, unless they are flattened against the wall of the parent colony. (Pl. XI, figs. 2 and 3; pl. XII, figs. 7, 8, 11 and 12; and pl. XIII, figs. 14, 15 and 16.) They lose this form only when approaching disruption. (Pl. XIII, fig. 17.) Not only are they without the somatic area, being without

all somatic cells, but the sperm platelets and the preceding generations of cells which produce them all develop with great uniformity, and all become finally mature at the same time. (Pl. XII, fig. 12; pl. XIII, figs. 14, 16, 17.) The only exception is the temporary irregularity in the sizes of the cells during some of the last divisions that form the sperms (pl. XIII, fig. 15); but this irregularity is temporary only, and has nothing to do with the perfect equality of all sides of the sperm sphere as such.

From all of these facts it becomes plain that the sperm formation of the *Volvox* we are describing is very different from even the types which most closely resemble it. If these sperm spheres are phylogenetically mere parthenogenetic daughter colonies it is plain that they are daughter colonies that have become so subordinated to the single function of sperm production that they stand to the parent organism upon the functional plane of a mere spermary. Only the tangled web of homologies prevents our so recognizing them at once. The facts of development will throw a little more light upon the question. To them we shall shortly return, but first a fuller description of the sperm spheres.

The number of sperm platelets in the sperm spheres follows very closely if not exactly the theoretical numbers 64, 128, and 256, there being these three sizes and these only. I have made many counts which give me sometimes the exact numbers, although it is difficult to avoid a certain range of error which is of course greatest with the highest numbers. These results may be checked somewhat by counting the numbers in the hemispheres in plate XIII, figures 14, 15, and 16. Plate XII, figure 12, may also be used. Figure 14 represents one-half of a large-sized sperm sphere in the spermogonia stage and will be found to show very close to 128 cells; figure 12 is a mature sphere of corresponding size and shows a similar number; figures 15 and 16 are of intermediate colonies and give approximately one-half the number of individual groups. Near the center of figure 16 a blurred space may be seen large enough to contain two sperm bundles. Under the microscope it did show these bundles, but they were disintegrating and plainly degenerate cells. It is probable that a few cells may degenerate at any stage and so reduce, in some cases, more or less the final number of sperm platelets. My count indicate this. Nevertheless the number seems usually regular. As to the frequency of these three sizes of sperm spheres, the smallest

are much the most infrequent, and while the largest are frequent, by far the greater number are of the intermediate size.

The 64-celled sperm sphere, in the spermogonia stage, is interesting, if we interpret it as a colony, for it reduces to a minimum hitherto not met with, the possible size of a *Volvox* aggregation. Klein regarded as such a minimum the small, sexually mature colonies formed within the parental coenobia in the special variation of *V. aureus* before mentioned. These were about 100 μ in diameter with approximately 180 to 200 individual cells, of which about a third became spermogonia ("Androgonidien") and developed into sperm platelets. The number 200 was the minimum, for the cells of a free-swimming colony, which his earlier research gave him. The diameter of these sperm spheres is not much less than 100 μ , even for the smallest size. The three sizes range from about 80 μ for the smallest to 180 μ for the largest. But the cell number of the smallest size is but a third of that in Klein's smallest colony and brings the cell number for a *Volvox* colony to but double that of *Eudorina*. Indeed the resemblance of some of these smallest sperm spheres, while in the spermogonia stage, to large compact colonies of *Eudorina* which chance to be in some of my preparations is striking in the extreme. Even the size and shape of the cells and their reaction to stains differ but little.

As to the genesis of these sperm spheres nothing is easier than to trace it throughout all of its stages except the very first, and even these are tolerably plain. As a glance at the plates will show, these sperm spheres develop usually, though not always, in the same coenobia and side by side with ordinary vegetative colonies. (Pl. XI, figs. 2 and 3; and pl. XII, figs. 7 and 8.) Their periods of development, moreover, coincide as a rule closely, though not exactly. For the examination of a very large number of cases discloses the curious fact that well nigh the first indication as to the ultimate character which the segmenting reproductive bodies within a coenobium are to assume lies in the fact that certain ones are one or two cell divisions ahead of the others, say, in the 16-cell or 32-cell stage as opposed to two, four, or eight. These slightly more advanced anlagen invariably, it seems, become the true vegetative colonies, while the slightly laggard ones, seeming at first sight to differ in no other respect from them, almost as invariably become the sperm spheres. The instances confirmatory of this rule are very numerous; those which deviate from it are few and usually, when they do

occur, are great deviations—cases of irregular reproduction. As to the enlarged cells which develop into these vegetative colonies, on the one hand, and into the sperm spheres on the other, I at first thought their appearance identical. And as we shall see later, in no other form of *Volvox* is the parity (homology) between the three forms of reproductive cells so close as in this type. Yet a further study of these cells showed evidence that a slight inner differentiation, accompanied usually with difference in size, had taken place. These cells, in general, measure from 30 to 36 μ . The more slowly segmenting ones are the smaller by about one to three microns, their nuclei are perhaps a trifle larger and, plainest of all, their cytoplasm is denser, the transparent area between nucleus and chromatophores being noticeably less. This somewhat denser character of the cells is evident throughout all the developmental stages in the sperm sphere.

These facts point strongly toward the interpretation that the sperm spheres are not daughter colonies with an extreme and precocious sexual development, but, on the contrary, are really spermatogonia, checked before their final division into sperms, and stimulated to undergo several generations of what we may call vegetative division. The phenomenon is evidently comparable to the isolated cases, to be described later, in which cells that had attained the full size and character of ova then began vegetative segmentation; although what the result of such segmentation may be I cannot say. Another fact indicates still more strongly this interpretation, *viz.*, the size of the cells throughout the entire development of the sperm sphere. At no time does this fall below 6 μ , whereas in the young vegetative colonies, after the first slower segmentation up to the 32-cell stage, it passes by rapid division to the small size of 3 μ long before the young colony has closed in to form a complete sphere. From this time the cells of the young vegetative colony increase slowly in size again throughout its entire growth period. (Pl. XII, fig. 10.) No such repeated division, rapid reduction, and slow increase in size occurs in the cells of the young sperm spheres at any stage, and it is the large size of the cells which renders them instantly recognizable among the young daughter colonies, however closely they may resemble these in general size and other respects. (Pl. XI, figs. 2 and 3; pl. XII, figs. 7 and 8.)

On the whole, then, my general conclusion in regard to the relationship of this form, which perhaps I may well state now, is that

it is not derived either from *Volvox tertius* or from the special form of *Volvox aureus*, to both of which it shows a superficial resemblance, but from the typical *Volvox aureus* by a variation of an opposite nature. Instead of precocious development with early maturing sexual cells, there has been an increase in vegetative growth, a retardation in the specialization, together with an increase in the number of the sex cells, that is, of spermogonia and finally of sperms. The facts which look the other way are the general form of the sperm sphere, which makes it closely resemble a colony, and cilia which it certainly bears at some stages of its development. But the spherical form is characteristic in some degree even of the sperm bundles; and cilia, likewise, probably occur, at least in some stage, in all volvox cells. It will be seen that nearly all the other characters of the form bear out, at least indirectly, this general view.

As to the number, size and structure of the sperms themselves, they agree in the main with those of *Volvox aureus*. The single sperm bundles contain invariably 32 sperms (pl. XI, fig. 12; pl. XII, figs. 16 and 17), agreeing with Klein's special form of *V. aureus*, but disagreeing with both *V. aureus* and *V. globator* as usually found. The numbers found in the former are usually 16 and 32, the variation occurring in one and the same individual. Klein found, rarely, as few as eight. *V. globator* commonly shows either 64 or 128 sperms in one platelet, while it is claimed the number may rise to 256. As to the whole number of sperms simultaneously ripened in a single coenobium, it greatly exceeds, in the form I am describing, anything hitherto found. The maximum number which I actually find matured in any one parent colony in my preparations is in a medium-sized individual whose sole content consists of eight ripe sperm spheres, all of the maximum size. Assuming each sphere to be, as it looks, perfect, and hence to contain 256 sperm bundles, we find the total number of simultaneously maturing sperms to be $8 \times 32 \times 256 = 65536$. I think this theoretical number very close to the fact in this case. Judging, however, from the number and size of young sperm spheres which I have seen in single coenobia, I estimate that coenobia must occur bearing over twice this number.

In form and inner structure of the sperms themselves, they agree fully with those of *V. aureus*. Overton¹ has shown that the sperms of *V. globator* and *V. aureus* differ markedly in structure: the for-

¹ E. Overton: "Beitrag zur Kenntniss der Gattung *Volvox*. Botanisches Centralblatt XXIX: 30, etc. 1889.

mer are slender with elongated nuclei and more or less laterally attached cilia; the latter are less differentiated, being less elongate, with spherical nuclei and terminal cilia. Careful attention to suitable bundles in figures 12, 16 and 17 will show that in this respect, as in a majority of minor characters, this form relates itself closely to *V. aureus*: the nuclei are spherical, the sperms compact and the cilia terminal.

Turning to the more general features of the *Volvox* under consideration, many other characters show themselves equally new, if less striking. Thus the numbers and numerical relations of the three sets of generative structures, eggs, sperm spheres, and vegetative daughter colonies, are again unique within the genus. The maximum number of vegetative colonies is about twice that found in any previously described form. *V. globator* shows regularly eight parthenogenetic daughter colonies. *V. aureus* is highly variable. Four is often given as the common number, although this may rise to six or seven under certain conditions. Overton, during long search, found eleven the maximum. Oltmann¹ gives twelve as the maximum for the genus, although Klein had already, in his extended research, raised the maximum in *V. aureus* to fourteen. Such numbers have, however, hitherto been wholly exceptional. With the form I am describing they are frequent, and with the form I shall describe at the close of this paper they may be multiplied five-fold. In my examination of the fresh material, I remember distinctly having counted 22 well-developed daughter colonies within one parent. In my slides at present I cannot find so high numbers among the developed daughter colonies. The greater proportion of the largest coenobia may have been ruptured before my preparations were made. But in the younger coenobia, both before and after birth, I find, not infrequently, over 20 enlarged cells which must certainly in many cases all become vegetative colonies. (Pl. XII, fig. 9 represents such a young coenobium with apparently 25, but really 24, reproductive cells.) How high these numbers run may best be shown by giving several concrete cases. A large coenobium, with ten daughter colonies of maximum development before birth, the largest measuring 210 by 240 μ , gives the following counts: one daughter colony showed but 16 enlarged cells, three showed 18, two 19, one 20, one 21, one 22, and one 23. Another coenobium, with nine daughters of 205 to 225 μ average diameter, showed four with 16

¹ Oltmann: *Morphologie und Biologie der Algen*. Jena; 1904.

enlarged cells, two with 17, two with 18, and one with 21. Another, with six daughters of about 225 to 240 μ average diameter, gives one with 17, two with 19 and three with 20. Yet another, with five daughters of the maximum diameter of 250 μ , gives the surprising numbers of 15, 23, 23, 24, 24. The highest number that I find after a moderate search is 25. There is no reason to think that in times of exclusively parthenogenetic reproduction this number would be reduced. More probably it would be augmented. In the case of my material, however, the more richly reproductive coenobia seldom remain exclusively vegetative.

In the number of ova or oosperms this *Volvox* again shows itself independent. *V. globator* shows, according to Overton, 12 to 40, usually about 30; according to Bütschli, about 50. *V. aureus* possesses, according to Bütschli, never more than 8; according to Overton, usually 5 or 8, sometimes 4 or even 3, and in partially vegetative colonies, even one. Klein figures as many as nine. I find a number intermediate between the maxima of *V. globator* and of *V. aureus*, 18 and 19 being the highest numbers at present found in my preparations. Numbers approximating these are common, although the number may fall in mixed coenobia as low as one. Obviously, here again, this form is closest to *V. aureus*, in that the number of egg cells has the same upper limit as has the number of vegetative colonies; while in *V. globator* the two show widely divergent relations. In size, however, the eggs of this form are smaller than those of *V. aureus* and resemble those of *V. globator*, being 51 to 54 μ as against 60 μ for *V. aureus*. The walls of the mature zygotes are again of an intermediate type. They agree with those of *V. aureus* and differ from those of *V. globator* and *V. carteri* in that they are plain instead of crenate or wavy. But they differ from those of *V. aureus* and agree with those of *V. globator* in that the cell is not asymmetrically but symmetrically placed within its inner wall. (Pl. XI, figs. 5 and 6.)

The numbers of the sperm spheres also range very close to those of the ova and of the vegetative daughter colonies. Frequently a single one is present in a parental colony bearing other reproductive bodies as well (pl. XII, fig. 8), while the maximum number may rise well up toward that of the ova or of ordinary vegetative colonies. Fourteen sperm spheres, together with two ordinary daughter colonies in one maternal coenobium (pl. XII, fig. 7), seems to be the highest number I have recorded, although I think higher ones occur.

The close approximation to parity between the number of primitive reproductive cells, which may develop into parthenogonidia, into ova, or into sperm sheres, is again a peculiarity of this *Volvox*. In *V. globator* and *V. carteri* the anlagen of eggs and sperms are about equal in number, but greatly surpass the maximum number of parthenogenetic cells. In *V. aureus* and apparently in *V. tertius* it is the true ova and the parthenogonidia that run in parallel numbers, while the anlagen of the sperms may exceed these many-fold. In the *Volvox* before me the numbers, at least the limiting numbers, of all are closely parallel. This parallel in numbers, taken with the close simultaneity in origin, which is the rule, and with the close, though not entire identity in structure, seems to the writer to have a not unimportant bearing on the vexed questions of homology between the different reproductive bodies in all members of the genus.

To make more complete as well as more detailed these relations between the various reproductive bodies, I will give the results of an examination of 100 independent coenobia taken serially as they occurred on three of my slides, the only ones rejected being such as were too young to admit certain determination of their reproductive contents. Of the 100 coenobia, 18 bore only vegetative daughters, the maximum number being 14 and occurring twice, the minimum being 5 and occurring but once, the average being 9.5. The number of exclusively female coenobia, *i. e.*, those containing ova or oosperms only, was five, the numbers being 7, 8, 14, 15, 16; average 12. No coenobia occurred among the 100 showing exclusively sperm spheres as reproductive contents, although such are not infrequent. (Pl. XII, fig. 11.) Likewise none occurred showing sperms and ova without the presence of vegetative offspring as well; such I have never seen. Over one-half of the colonies, 55, showed the combination of sperm spheres with vegetative daughter colonies. The maximum number of sperm spheres in one of these coenobia was 11 and occurred twice; the minimum number one, which occurred fourteen times; the average was 4. Among the vegetative daughter colonies of these same coenobia the maximum number was 14, occurring but once, and the minimum number 1, occurring but once; the average 7. The last possible combination of the reproductive bodies was represented by 12 colonies which contained vegetative daughters together with both sperm spheres and eggs or oosperms. These were plainly larger than the average of the others. The extremes among the eggs (or oosperms) being 1 and 7, the aver-

age being 3.3. The extremes among the sperm spheres being 1 and 8, with the same average; while among the vegetative daughters occurred the numbers 2 and 13, with an average of 7.2. These facts are fairly typical, although the number of coenobia examined is of course too low to represent other than an approximation to the real numerical relations involved. The coenobia containing eggs alone were never large; those containing all three classes of reproductive bodies usually were large; those containing sperm spheres together with ordinary vegetative colonies were of all sizes. A rather novel fact, however, is the tendency of these latter coenobia to one extreme or the other. One finds repeatedly a single sperm sphere among a number of ordinary young (pl. XII, fig. 8), and not infrequently the opposite relation (pl. XII, fig. 7), while evenly balanced coenobia are less frequent. But two of the above 55 showed an equal number of ordinary daughter colonies and of sperm spheres. As to the time of maturing of ova and sperms, the former are, in the rule, fertilized and have become thin-walled oosperms before the sperm spheres of the same parent coenobium have become fully mature. This follows from the simple fact that the primitive sex cells start, as a rule, almost simultaneously, and it is obviously a shorter route to develop into a ripe ovum than to pass through both the growth and the differentiating processes necessary for the production of a complete sperm sphere with its multitude of differentiated sperms. Notwithstanding this, instances occur of the simultaneous ripening of ova and sperms, as in the coenobium represented in plate XI, figure 3, where a ripe ovum, apparently unfertilized, is in practical contact with a colony of very fully developed sperm platelets. In such cases as this the anlage of the sperm sphere undoubtedly started ahead of that of the ovum. Such non-simultaneity, though as I have said, not the rule, is not very infrequent among all the classes of reproductive bodies.

As to the size of the adult colonies of this *Volvox* I can furnish less exact data, all of the large colonies in my preparations having been at least somewhat flattened. Measurements which I made on the living material are not now at hand. They showed, however, that the size exceeded the usual maxima given for any species of the genus. Oltmann gives the highest maximum I have seen, 1 mm. It is safe to place this as the upper limit of the present form. The lower limit for colonies containing mature reproductive bodies is much above the usual limit for *V. aureus*, 680 μ being the lowest

measurement I have found in my preparations, from which something may be subtracted for a little flattening, leaving as a minimum, say, not less than 500 μ . Klein found full-grown *V. aureus* as small as 175 μ .

In contradistinction to this large size of the adult coenobia, the daughter coenobia are never as large or as fully developed as frequently occurs in *V. aureus*. Doubtless this goes hand in hand with the increased number of the daughter coenobia, for the same variations are carried to an astonishing degree in the next form I am to describe. The maximum size of the daughter colonies before birth is, as I have indicated above, about 250 μ , and the smallest free colonies are but now and then a little below this. The relative retardation of the daughter colonies, say at birth, is farther shown by the fact that the parthenogonidia in this form never segment before the daughter colonies containing them leave the parent coenobium. This is very common in the ordinary forms. But in the type I am describing segmentation of the reproductive cells only takes place after considerable growth in the free state. Measurements on a number of young colonies and their contained parthenogonidia show this plainly. A few colonies are found above 400 μ in which but part of the parthenogonidia are beginning to segment, but the majority show some segmentation at 350 μ . Only daughter colonies which contain very few reproductive cells, and which doubtless escaped from smaller parents at a correspondingly smaller size, show segmentation at 255 μ or possibly at even less. The reproductive cells—parthenogonidia, etc.,—within the largest unborn daughter colonies measure but 15 to 18 μ , while the regular size in the free colonies that are beginning to show segmentation is, as I have said, exactly twice this, *viz.*, 30 to 36 μ . These last figures are on the whole very constant, but in rare cases a singular variation occurs—a further retardation. I find in a very few coenobia cells in various stages of division (pl. XIII, fig. 18), which, before dividing, have reached nearly the size of ova and oosperms, *i. e.*, 51 μ . Such phenomena are very striking, and suggest the possibility that these may not be parthenogenetic cells, but fertilized ova which, instead of entering the usual resting stage, are developing at once. This is, however, but conjecture, and is less probable than the hypothesis of mere delay with continued vegetative growth.

Concerning the number of cells in the colonies, I am unable to give accurate figures. To count the larger colonies correctly is not

possible, and estimates—*e. g.*, according to the method of Klein—all imply the sphericity of the colonies. As mine are flattened to a certain though unknown extent, estimates become precarious. Such as I have made, however, indicate that the number of cells is well within the limits given by Klein for *V. aureus*. Indeed I think that nothing comparable to his widest extremes—200 to 4400—occurs. Certainly nothing is found approaching his lower limit for free colonies. Well grown daughter coenobia like plate XII, figure 13, show about 1700 or 1800 cells, as may be verified by counts on the figure. The largest colonies probably hardly exceed 3000. The extra large size of these colonies is plainly due to the development of the gelatinous matrix.

Touching the finer structure of the colony, I shall omit such points as are not characteristic of this form as well as those which my preparations are not adapted to disclose. The size of the individual cells in adult colonies ranges from 6 to 10 μ , most of them being of the smaller size.¹ The distances separating them may be as great as 50 μ , but are usually from 28 to 40 μ . The vegetative cells in daughter colonies at birth are about 5 μ and increase to nearly or quite full size by the time the parthenogonidia enter on division. In shape these cells are more nearly spherical than is usually the case even in *V. aureus*, resembling most of all the figure which Arthur Meyer gives for *V. tertius*. Moreover, a relationship to this species is further shown in the utter absence, as far as my investigation goes, of connecting strands between the separate cells. Meyer failed to find such connections only in *V. tertius* in the adult condition, the younger colonies still showing them. I fail to find them at any stage whatever. It is true I have not employed the technique resorted to by Meyer, but I used reagents which ordinarily suffice, and on living material. Many of my permanent preparations also seem well adapted to the purpose, especially material fixed in the diluted Flemming's and strongly stained with rose bengal. This gives an admir-

¹ The larger cells are seldom wholly wanting in the larger coenobia, which fact suggests the possibility that they are, in reality, another and much later generation of reproductive cells. Such an interpretation would imply the probability that this *Volvox* does not always die after the birth of one brood of daughter colonies, but may live and develop another. My preparations show a number of large coenobia destitute of ordinary contents, yet evidently no longer ruptured. These, therefore, suggest the same possibility; while the study of the second form of *Volvox* described is still more suggestive of such a possibility.

able fixation, seemingly devoid of shrinkage, and the stain takes heavily in the cytoplasm while leaving, as most stains do, the matrix perfectly colorless. Yet neither in old nor younger colonies at any stage can I discover a trace of the connecting fibers, even under a Zeiss apochromatic. The connecting strands in *V. aureus* are said to be of about the same diameter as the cilia. Several observers have failed to demonstrate them, but in some such cases their preparations have failed to show cilia as well. In mine the cilia, both within and without the matrix, are plainly visible with ordinary magnification. Doubtless more investigation will be necessary before concluding that these structures, supposably so characteristic of the genus, may be entirely wanting. Meyer would not assume their real absence in adult *V. tertius* despite his elaborate technique and his total failure to demonstrate them. Yet his refusal to accept his own evidence seems to have been for rather theoretical reasons. No one claims that the closely allied genus *Eudorina* possesses them. Yet it shows the same phenomena of apparent coordination, etc.

Concerning the structure of the gelatinous walls and intercellular substance I will say little, because I have not used the technique which Meyer has shown to be necessary to discover the details of the structure. Most of the reagents used by me were rather ineffectual in this regard. They did little more than emphasize the structure which was faintly visible in the younger living coenobia, *viz.*, a separation of the surface into clearer, spherical areas, about the individual cells, and grayer, intervening paths of connecting substance. This is shown to some extent in several of the figures. (Especially pl. XII, fig. 10.) Such surface fields are wholly unlike *V. globator*, but resemble those of *V. aureus*, and are identical with those given by Meyer for *V. tertius*. Other indirect reasons lead me to suspect that so far as the wall is concerned, *V. tertius* is the most nearly allied to the form I am describing.

A few further words might now naturally follow, as to the systematic position of this *Volvox*, whether it constitute a new variety (mutation?), species, or genus? But I will postpone this consideration until I have briefly described the second form which came under my observation.

I owe the discovery of this second form of *Volvox* again to my pupil and assistant, Mr. George R. LaRue of Crete, Nebraska. It was not in sexual reproduction at the time (September) when it was discovered. But despite this fact it is little less noteworthy than

the form just described and is especially interesting taken in connection with it, as certain lines of variation which the first form shows but moderately are in this one carried to surprising extremes. Its size attracted the attention instantly, even when in the pond. I judged that many of the colonies could not be less than 2.5 mm. in diameter.¹ In well preserved formalin material, showing a little shrinkage, I readily find coenobia over 2 mm. in diameter and the majority closely approach this limit. I examined thirteen colonies taken at random before I found one as small as 1.8 mm. The average size of this *Volvox*, then, judged by its adult colonies, is more than twice the size previously recorded for any species of the genus, and three to four times the average size recorded for *V. aureus*. The size, however, was dependent in this case even less than in the preceding upon an increased number of cells. On the contrary I find the number very low, often below a thousand even in the large colonies and seldom much above it. They are about 12 μ in diameter, as against 7.5 to 8.5 μ for the preceding form, and are separated by varying intervals of from 50 μ to as much as 200 μ , in comparison with 28 to 50 μ for the preceding form. If connecting strands of cytoplasm of quite invisible fineness (I can make out no trace of them) connect these cells, they are surely something of a phenomenon.

A consequence no doubt of the large size and scattering cells of these colonies was their extreme fragility. I lost most of the material of my collection by entrusting it to a fixing fluid which has often given me admirable results with related forms—leaving the matrix of *Eudorina*, for example, wholly unharmed. But these over-expanded colonies were quite unable to withstand its action. Correlated also no doubt with the size of these colonies, though not wholly thus explicable, was the most surprising feature they disclosed, *viz.*, the number of parthenogonidia or of vegetative colonies they contained. In not a few cases both the parthenogonidia and the young colonies had been partially or wholly destroyed by some agency, possibly a parasite. In such colonies the remaining number of daughter colonies, for example, might sink to any number, and

¹ Professor Charles E. Bessey, of the botanical department of the University of Nebraska, informs me that he has also observed *Volvox* colonies in this vicinity which were at least close to 2 mm. in diameter. This is interesting as showing that the form I am about to describe is not an isolated or accidental variation.

in one instance one alone remained in a developed healthy condition. Omitting such colonies, the count of ten instances gave the following numbers of parthenogonidia or daughter colonies: 10 (very old and probably not perfect), 15, 29, 30, 33 (not full number), 35, 41, 49, 49, 71. It is not probable that these numbers represent the maximum,¹ since the material examined was insignificant in amount. But as they stand they are wholly without precedent, trebling, as they do, the number found in the preceding form and multiplying five or six-fold that hitherto found in any species or variety. As indicated, this high number of parthenogenetic reproductive bodies may well be correlated with the large size of the colonies, or perhaps with the wide sundering of the cells and absence or functional weakness of the connecting strands allowing of less specialized concentration of nutritive excess upon a few individuals. That it was not purely a matter of size, however, is shown by the fact that the reproductive bodies are not, as usual, confined to one-half of the volvox sphere, but, in case of the higher numbers at least, were distributed over two-thirds or four-fifths of the surface (pl. XIV, figs. 19, 20, 21 and 23), simulating the distribution of the sperm bundles in *V. aureus* when these are very abundant.

With the great number of the daughter colonies and the feeble nutrition of the flimsy parent coenobium was no doubt correlated two of the remaining peculiarities of the form, *i. e.*, the insignificant size of the daughter colonies and the complete retardation, until after birth, of their reproductive cells. None of the daughter colonies which I examined were above 150 μ in diameter. The majority measured but 125 μ or even less. I deemed these at first to be merely very immature parthenogenetic progeny. But despite the large size of the coenobia and the fact that some of them appeared to have discharged a part or all of their contents, I could find none with larger daughters. This led me to question whether this were not the size at which these colonies were freed from the parent sphere, and such seemed finally the inevitable conclusion. Unfortunately but few immature, free colonies could be found. The smallest, however, measured but 279 μ and yet was plainly an independent, free colony. Its individual cells were 7 μ in diameter and were already separated by intervals of 9 to 15 μ . (Pl. XIV, fig. 25.)

¹In the course of photographing the coenobia shown on plate XIV another was found in the same small lot of material showing 78 parthenogonidia or young colonies. (Pl. XIV, fig. 20.)

Not only, then, do the daughter coenobia here escape at a very small size as compared with that of the adult, but they are equally or even more retarded with regard to their reproductive cells. Not one of the developing daughter colonies showed a trace of differentiation of parthenogenetic cells of the next generation (pl. xiv, fig. 24), while in the smallest free colony, above mentioned (fig. 25), they were just making their appearance, 30 of the component cells having enlarged to from 9 to 10.5 μ , as compared with 7 μ for the remainder. As we have seen, in ordinary species the parthenogenetic ova differentiate, reach maturity, and even begin to divide before the birth of the daughter coenobia containing them. In the special form described above they reach but half their full diameter by the time the young coenobia are freed. While here in this form they are not even distinguishable at this period. Their time of maturity and division is indeed not until apparent maturity of the coenobium, to judge by the material examined by me. A number of almost the largest colonies (fig. 19) showed undivided, though mature, anlagen; in others they were in early stages of segmentation (fig. 20), while in the oldest coenobia (figs. 21 and 22), containing young colonies of full size, there might still be present few or many parthenogenetic cells of an altogether later generation. This variation constitutes almost as striking a change of habit for the genus as did the mode of developing male gametes in the preceding form. It would seem, too, of doubtful advantage, for these large fragile colonies might easily be destroyed before the maturity of their late-developing progeny. It is possible, as I have indicated before, that more than one generation of young is here produced.

But one further peculiarity was noticed, *viz.*, the early age at which the increase in gelatinous matrix began to separate the component cells of the young daughter colonies. Ordinarily this takes place hardly at all before their birth. Here it begins apparently as soon as the young colonies are closed spheres. Unclosed colonies showed the cells compactly pressed as usual, and this stage was sometimes 60 μ in diameter. Complete daughter colonies were found, however, in the same parental colony, as small as 75 μ , in which the separation had already begun, the cells being completely rounded and none of them in contact. As above noted, in the smallest free colony, of 279 μ (pl. xiv, fig. 25), the intervals between the cells have already increased to more than their own diameters. The final result of this early-begun production of intercellular material

is the production of colonies which, under the microscope, are scarcely recognizable as volvox aggregations. Indeed many of the older coenobia would not have been so recognized without study (fig. 22). They had become practically motionless, were befouled by adherent particles, their component cells, when not obscured, showing only as pale green dots scattered about the surface.¹ So large, thin-walled and delicate were they that when resting in water on the bottom of a watch glass they were flattened somewhat by their own weight, filling more than the low power field of the microscope and responding to every jar by vibrations and minor changes of form. Yet even such colonies as these might contain at least some healthy daughter aggregations. (Pl. xiv, fig. 22, near left and lower margins.)

What of the affinities of these two forms of *Volvox*? It is embarrassing at the start that there are two of them. Are the two distinct or only diverging forms of one species. They are certainly different enough to be distinct. Yet there are many points of resemblance, and the extreme variation of the second from the first does but carry out some of the same lines of divergence which separate this from *V. aureus*. It is safest to assume that the two forms are closely allied. An added reason for this is found in the conditions under which they occurred, the second form having developed in much smaller numbers and in deeper water than the first. And Klein has shown that *V. aureus* differs greatly in size, even in similar and adjoining ponds, according to its sparsity or abundance. The least crowding reduces its dimensions very much. This fact explains something, if but little.

Taking, then, the two forms as, provisionally, one, what is their relation to the genus *Volvox* and its previously described species? Their relation to them is obviously close. Yet it is equally evident that they do not fit into any previous specific definitions, and, no less, that they quite transcend the definitions previously given for the genus. This is true whichever of the two interpretations we put upon the peculiar reproductive phenomena described for the first form. Still this fact does not demonstrate this new-found *Volvox*

¹ Without careful attention many of the component cells of the colonies may well be missed in all the coenobia, except the last two, of plate xiv. They may be seen however as small dots about 2 mm. apart. Others have been retouched and somewhat distorted. Figures 21 and 22 show them only near the center of each.

to be even a new species. For generic distinctions may, no doubt, be overstepped as easily by variation as may specific ones. Witness the case, already mentioned, in the same family, that the new genus (as supposed) *Pleodorina* intergrades perfectly with its well known relative *Eudorina*. So these peculiar types of *Volvox* may well prove to be only extreme variations ("mutations," if you will?) of *Volvox aureus*. Very pronounced variations they are, sharp and clean and influencing numerous characters, well up to the mutation standard. Should such prove to be the case, it would certainly be the happiest consummation, for it would give us in this interesting family of organisms a species of almost unheard-of variability and thus open the way for promising experimental work.

In conclusion, I wish especially to thank Dean Charles E. Bessey, of the botanical department of the University of Nebraska, for his most courteous assistance in searching for the literature of the subject. The bulk of this lies on the botanical rather than the zoological side.

EXPLANATION OF PLATES

All of the figures are from photographs made by the simple, if somewhat unsatisfactory, expedient of a "Brownie" camera inverted over a Zeiss or a Leitz microscope. The unsightly quadrangular areas are the result, not alone of an effort to save space in the plates, but of the fact that the camera would not cover the full width of the larger microscopic fields. This latter is indicated by the curved corners.

Plate XI

FIRST FORM OF VOLVOX DESCRIBED

Fig. 1. A medium-sized coenobium containing five egg cells (one partially obscure) and thirteen daughter coenobia, within which can be seen the numerous anlagen of the next generation. Groups of minor organisms—*Euglena*, *Pandorina*, *Eudorina*, etc.,—are adherent to the colony, or in the field. Magnification about 56 diameters.

Fig. 2. A medium-sized coenobium containing ten immature oosperms, one daughter colony (near lower margin) and three sperm spheres in different stages of development. The one farthest to the right is a medium-sized sperm sphere showing platelets of mature sperms; to the left of this is a large-sized sphere of dividing spermogonia, while above and to the left is another medium-sized sphere of undivided spermogonia. Groups of minor organisms in the field and adherent to the colony, as in the last figure. In upper right-hand corner portion of a young free colony with reproductive cells still undivided. Magnified about 37 diameters.

Fig. 3. Small to medium-sized coenobium containing six daughter coenobia, five apparently unfertilized ova, and two sperm spheres of fully matured sperms. Magnified 37 diameters.

Fig. 4. Small coenobium with 18 young oosperms. Portion of larger coenobium with mixed contents and adherent groups of organisms above and to right. Magnified about 37 diameters.

Fig. 5. Medium-sized coenobium (much obscured by groups of *Trachelomonas*, etc., as above) containing 17 mature oosperms. To left and below, portion of still larger coenobium with very large daughter. The spherical body in this latter is not related to the volvox. Magnified 65 diameters.

Fig. 6. Detail from the last. Magnified 319 diameters.

PLATE XI

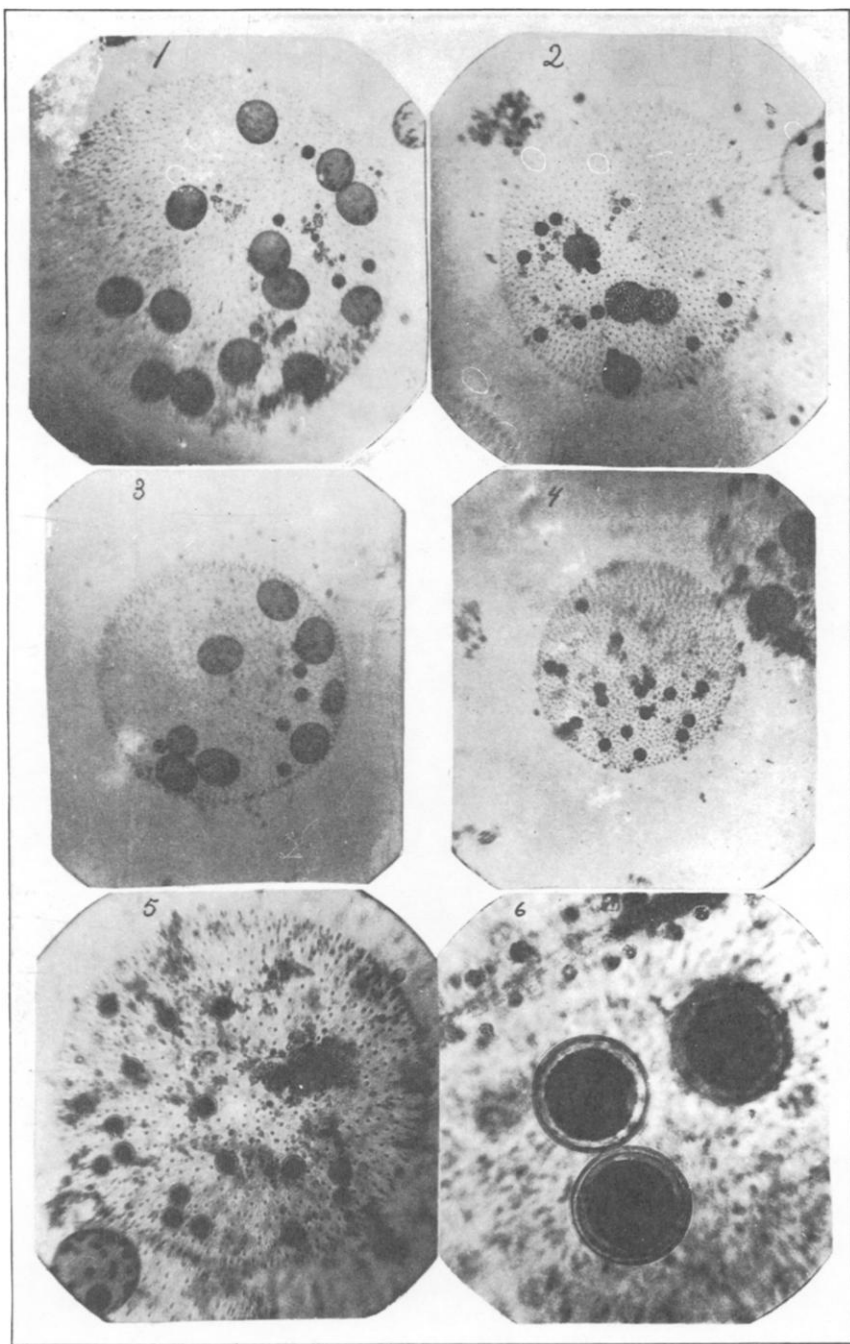


PLATE XII

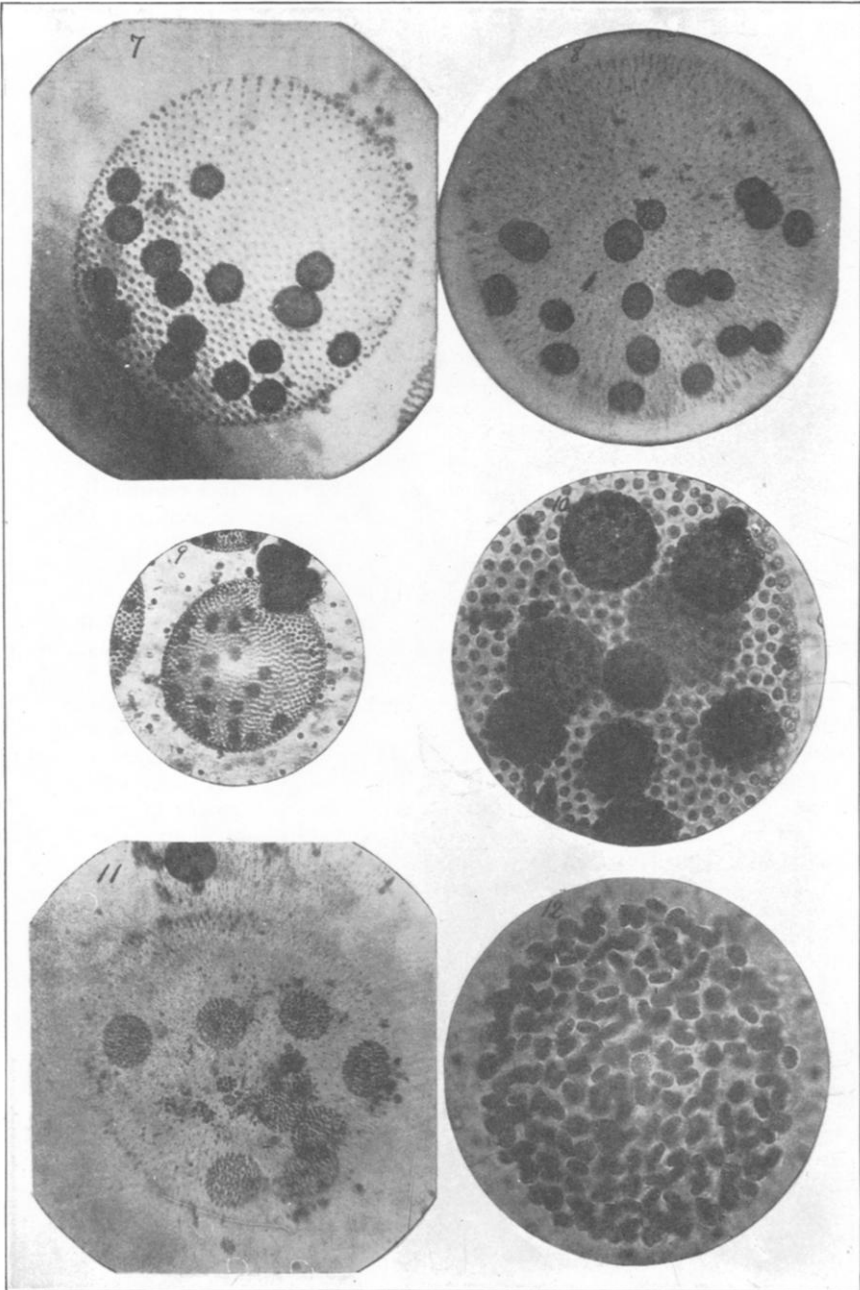


Plate XII

Fig. 7. Immature coenobium containing 14 young sperm spheres and two ordinary daughters. These may be distinguished by their even outline, and one by its ellipsoid form and larger size. Magnified about 74 diameters.

Fig. 8. Coenobium containing 17 ordinary daughters and one young sperm sphere. Euglenas, etc., adhere to the exterior of the colony. Magnified about 56 diameters.

Fig. 9. Large daughter colony, with small portions of two others; seen through the wall of the parent. It contains 24 undifferentiated reproductive cells; there appear to be 25 but one is a similarly sized trachelomonas. The four large cells which obscure a portion of the colony are extraneous. Magnified about 108 diameters.

Fig. 10. Portion of young free coenobium which contained nine very young daughter colonies and five very young sperm spheres. Four of the former are shown, mainly in upper half of the figure; their cells are already very small. Four of the young sperm spheres show in lower half of the figure, together with a part of a fifth. They show cells about the size of those of the parent colony. The figure also shows the characteristic areas in the gelatinous wall of the parent coenobium. Magnified about 217 diameters.

Fig. 11. Medium-sized coenobium containing eight of the largest-sized sperm spheres, all with fully mature sperms. Extraneous groups of organisms as before adherent to surface of coenobium. Portion of another coenobium above. Magnified about 37 diameters.

Fig. 12. Detail from the last, *i. e.*, single sphere of sperm platelets situated, in last figure, near left side of the parent coenobium. Magnified about 217 diameters.

Plate XIII

Fig. 13. Large daughter coenobium, photographed through the wall of the parent, the cells of which may be seen in the field as well as overlying the younger colony. The daughter colony is seen from one end and appears, therefore, spherical; its enlarged reproductive cells are somewhat greater than those of the parent coenobium. Magnified about 319 diameters.

Fig. 14. Large-sized sperm sphere in spermogonia stage; from same parent coenobium as the last. Magnified about 319 diameters.

Fig. 15. Medium-sized sperm sphere, the units of which are undergoing their final segmentations. The cells within the individual groups vary in size owing to a varying rate in segmentation which is, however, soon overcome. A portion of a daughter colony shown also; both photographed through the parent coenobium, some of the cells of which show in the figure. Magnified about 319 diameters.

Fig. 16. Medium-sized sperm sphere of completely developed sperm platelets. The wisps of cilia faintly visible in places, as also, in some cases, the spherical nuclei of the individual sperms. Each bundle contains 32 sperms. The whole aggregation was freed from the parent coenobium by pressure. Magnified about 319 diameters.

Fig. 17. Another sperm sphere, like the last, but showing the beginnings of disruption while within the parent colony, the cells of which are but faintly in focus. Three sperm bundles had escaped from the aggregation and were free within the coenobium; they are not shown. Nuclei plainly visible in some bundles. Magnified 319 diameters.

Fig. 18. Detail from a large, but young coenobium showing unusual instance of very large reproductive cells undergoing segmentation. Compare their size with the similarly magnified zygotes in plate xi, figure 6. Magnified about 319 diameters.

PLATE XIII

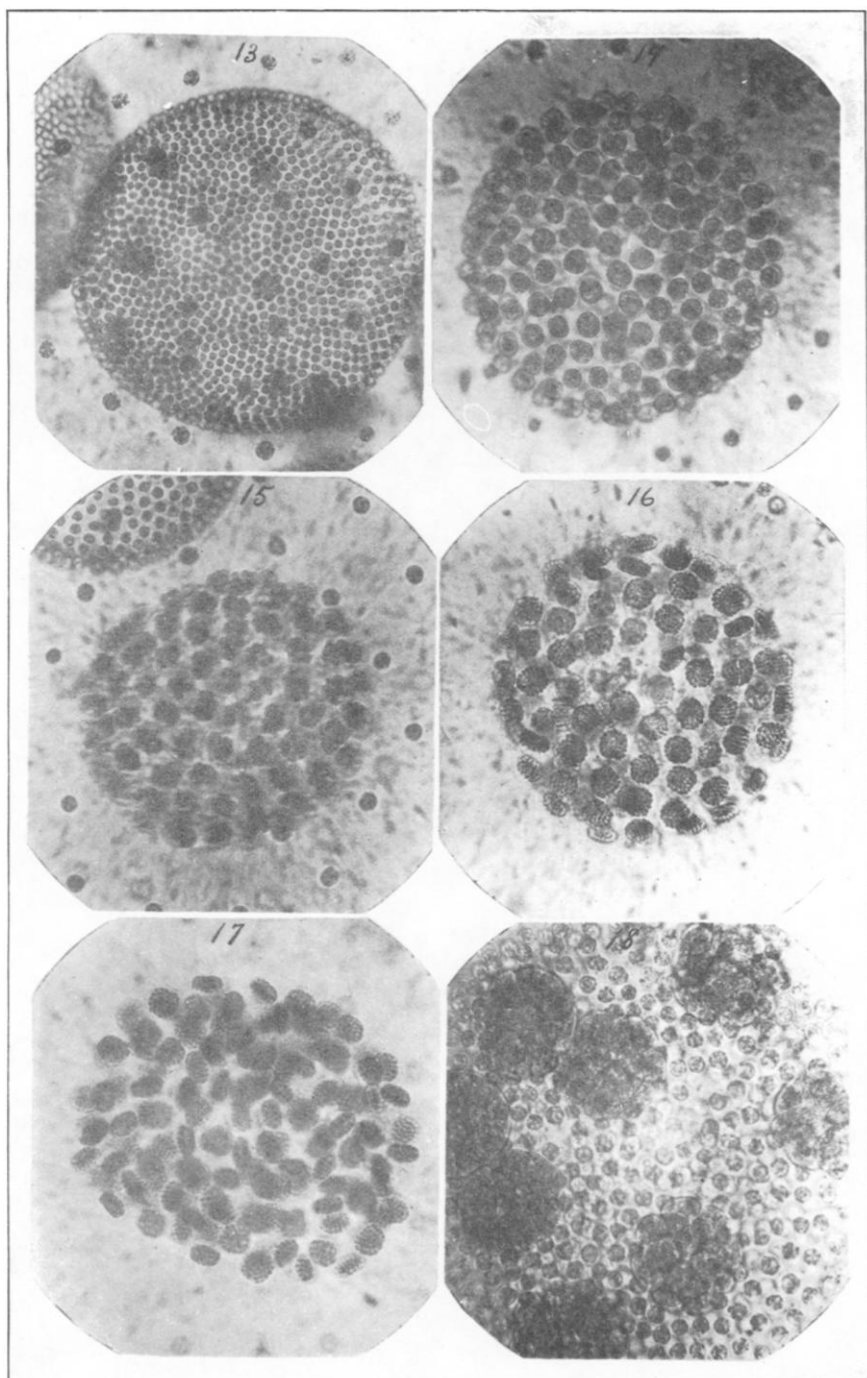


PLATE XIV

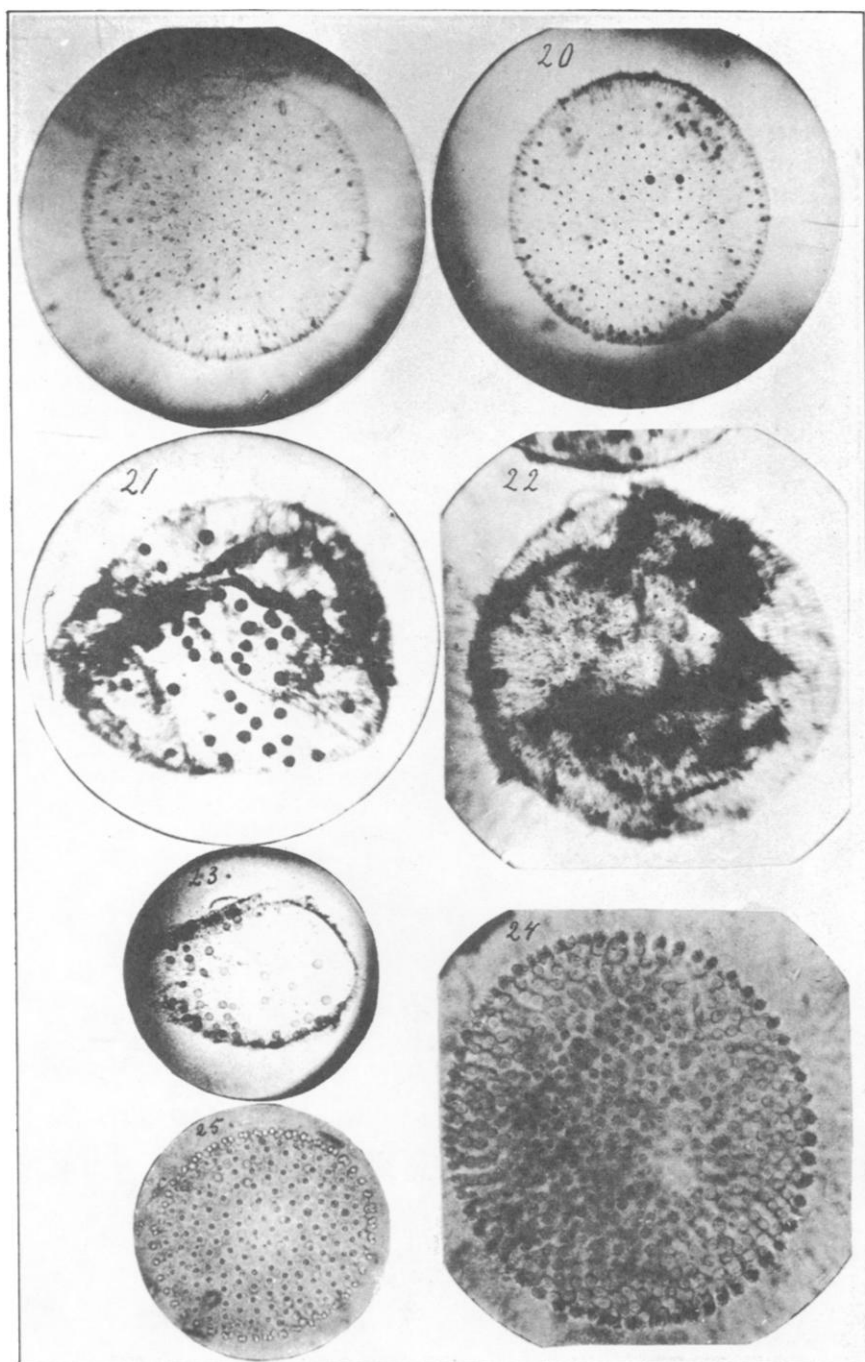


Plate XIV

SECOND FORM OF VOLVOX

Fig. 19. Typical colony. Some of its individual cells are only seen upon careful attention, showing a little less than 2 mm. apart. Others have been retouched by the engravers so as to exaggerate their size and somewhat distort their form. The larger black dots, 30 or more in number, are the parthenogonidia, unsegmented or in early division stages. Only a portion of them were in focus. Magnified about 17 diameters.

Fig. 20. A colony much like the last, but showing maximum number of reproductive bodies found—78. A perfect count is not possible in the figure but was easy under different foci. The two larger bodies are well grown daughter colonies (fig. 24); of the others, one was an undivided parthenogonidium, the others from the two-cell to approximately the 64-cell stages. Many of the cells of the colony are nearly or quite invisible; others have been retouched as in last figure. Magnified about 11 diameters.

Fig. 21. Large coenobium containing 49 well developed daughters, one much smaller, unclosed daughter colony, and six young parthenogonidia (easily recognizable by their strong staining reaction) of two to three times the diameter of the vegetative cells. The last two classes of bodies do not show in the figure. The daughter colonies are somewhat distorted by the retouching done by the engravers. The wrinkling of this coenobium in the preserving fluid displays the extreme tenuity of the colony membrane. The individual cells are visible but here and there as minute dots. Magnified about 17 diameters.

Fig. 22. An old coenobium characteristic of much of the material collected. Most of the cells obscured by the light layer of adherent debris. They may be seen, however, near the center of the colony where a few have been slightly retouched. As sole reproductive content the colony contains two large healthy daughters (below and to the left), four healthy, undivided parthenogonidia and a few that were degenerating. Magnified about 22 diameters.

Fig. 23. Another colony much like figure 21, but containing 71 well developed daughters most of which may be counted in the figure. Only a few of the individual cells of the colony may be seen. Magnified about 13 diameters.

Fig. 24. Daughter colony magnified to show early separation of cells and entire absence of reproductive differentiation. Photographed through the parent coenobium. A single cell of the overlying parent colony shows above and to the left of the center. Magnified about 319 diameters.

Fig. 25. Smallest free coenobium found. Showed the beginning of the differentiation of reproductive cells, 30 in all. Magnified about 108 diameters.

PLATE XV

